

**BIOLOGY AND IMMATURE STAGES OF *SETACERA ATROVIRENS*,  
A GRAZER OF FLOATING ALGAL MATS  
(DIPTERA: EPHYDRIDAE)<sup>1</sup>**

B. A. FOOTE

Department of Biological Sciences, Kent State University, Kent, Ohio  
44242.

---

*Abstract.*—Information is presented on the life history and larval feeding habits of *Setacera atrovirens* (Loew), a common and widely distributed shore fly species in lentic freshwater habitats. Adults and larvae are associated with floating algal mats where the larvae feed rather non-selectively on algal cells, including those of various blue-green genera. The egg, mature larva, and puparium of *S. atrovirens* are described and illustrated.

Miscellaneous observations on the habitat distribution, life cycle, and larval feeding habits are given also for *S. durani* (Cresson) and *S. pacifica* (Cresson).

---

The family Ephydriidae, shore flies, consists of at least 1200 species in the world (Rohdendorf, 1974), with over 400 species in 68 genera being recorded from America north of Mexico (Deonier, 1979). This vast fauna is reflective of the large amount of adaptive radiation that has occurred within this family of wetland-inhabiting flies. Among the radiations into different habitats has been the invasion of floating algal mats by at least three Nearctic genera of the tribe Ephydrini of the subfamily Ephydrinae. Adults of species of *Cirrula*, *Ephydra*, and *Setacera* typically are found on the surface of the shallow water of lake margins, ponds, and marshes. Larvae of several of these species have been collected repeatedly from floating or partially submerged mats of filamentous algae, although they may be actually feeding microphagously on the interstitial unicellular algae growing within the filamentous matrix (Brock et al., 1969; Collins, 1975; Simpson, 1973).

The biology, life history, and larval feeding preferences of certain of the algal mat-inhabiting species have been elucidated previously. Aldrich (1912), Beyer (1939), Brock et al. (1969), Collins (1975, 1977, 1980a, 1980b), Hennig

---

<sup>1</sup> Research supported by NSF grant DEB-7912242.

(1943), Johannsen (1935), Nemenz (1960a, 1960b), Ping (1921), Simpson (1973, 1976, 1979), Trägårdh (1903), Wirth (1971, 1975), and Zavattari (1921) have presented information on species of *Ephydra*. Apparently the only references to the immature stages of *Cirrula* are those of Mathis and Simpson (1981) and Simpson (1973) dealing with the life history of *C. gigantea* Cresson, a species inhabiting algal mats in salt marshes along the northeastern coast of North America. The only author who has published biological information on Nearctic species of *Setacera* is Johannsen (1935), who illustrated the immature stages of *S. atrovirens* (Loew) and *S. needhami* Johannsen. Beyer (1939) discussed in considerable detail the ecology, life cycle, and larval morphology of an European species, *S. micans* (Haliday) (as *Ephydra*).

The genus *Setacera* currently contains eight species in the Nearctic Region (Mathis, 1982), one in the Neotropics (Wirth, 1968), one in the Afrotropical Region (Cogan, 1980), and five in the Palaearctic Region (Wirth, 1975). *Setacera atrovirens* is widely distributed in North America, occurring between 55° and 105° west longitude and 38° and 49° north latitude (Mathis, *in press*). In contrast, *S. durani* (Cresson) has been recorded primarily in the Southwest, and *S. pacifica* (Cresson) apparently is known only from the western states and provinces (Wirth, 1965).

This publication is the fourth in a series of papers devoted to ephydrid species whose larvae can utilize blue-green algae (Foote, 1977, 1981a, 1981b). The present paper gives life history data and discusses the larval feeding habits of *S. atrovirens*, a common and widely distributed species in freshwater lakes, ponds, and marshes. Additionally, the egg, mature larva, and puparium of that species are described and illustrated. Fragmentary biological observations are also given for *S. durani* and *S. pacifica*.

#### MATERIALS AND METHODS

Most of the field observations on *S. atrovirens* were obtained near Kent, Ohio, in Portage County. Supporting observations for this species and for *S. pacifica* were obtained along the south shore of Flathead Lake east of Polson, Montana, in Lake County. Most of the field work dealing with the latter species was conducted at a highly alkaline pond located 5.0 miles south of Ronan, Montana, on the Ninepipes Wildlife Refuge.

The laboratory rearings were carried out in an environmental chamber programmed to give a photoperiod of 15L:9D and a temperature of 22°C ( $\pm 1^\circ\text{C}$ ). Monocultures of most of the algae used in the larval feeding tests were obtained from the University of Texas Culture Collection of Algae (Starr, 1978). Each algal monoculture was established on a nutrient agar substrate in sterile petri plates, and feeding tests were performed as given in Zack and Foote (1978). Monocultures of algae utilized in the tests, along with their UTEX strain numbers, are listed below. Species lacking UTEX

numbers were obtained from the phycology laboratory at Kent State University.

### Cyanophyceae

*Anabaena variabilis* (B-377)

*Anabaena* sp.

*Cylindrospermum* sp. (LB-942)

*Gloeocapsa* sp. (795)

*Lyngbya* sp.

*Nostoc commune* (584)

*Oscillatoria chalybea* (B-386)

*Oscillatoria tenuis* (B-428)

*Phormidium* sp. (1540)

*Synechococcus leopoliensis* (625)

### Chlorophyceae

*Chlamydomonas* sp.

*Chlorella vulgaris* (29)

### Bacillariophyceae

*Navicula pelliculosa* (668)

### Chrysophyceae

*Botrydiopsis alpina* (295)

## LIFE HISTORY OF *SETACERA ATROVIRENS*

Adults of *Setacera atrovirens*, like those of most other species of the tribe Ephyrini, are typically found on the surface of shallow water of small ponds, marshes, and lakes. They have elongated tarsi and straight claws, adaptations which permit adults to move over the surface film in a manner resembling that of the water striders of the family Gerridae (Hemiptera). The mouthparts are rather broad and fleshy and apparently allow adults to lap up microorganisms from the water surface. Deonier (1965) recorded adults as common in the floating algal-mat habitat and rare on muddy shores in Iowa, while Scheiring and Foote (1973) collected specimens only in the mud-shore habitat in Ohio. In contrast, I have found adults primarily on floating algal mats and only rarely on muddy shorelines.

Deonier (1972) in a study of the gut contents of adult Ephyridae reported that diatoms and other algal cells were about equally represented in guts of *S. atrovirens*. I have observed adults of *S. atrovirens* applying their mouthparts to the surface of algal mats and subsequently found cells of numerous algal genera in their alimentary canals. Adults fed readily on a variety of algal monocultures in the laboratory but survived longest on a diet of *Na-*

*vicula pelliculosa*, although good survival was obtained also on cultures of *Anabaena variabilis* and *Chlamydomonas* sp. Adults died within 2 or 3 days in pure cultures of *Chlorella vulgaris*.

The premating period varied between 2 and 4 days ( $n = 4$ ). No overt courtship behavior was observed, and males seemingly attempted to copulate with any suitably sized individual, including other males. Males were rebuffed by all adults of the wrong species, by males of *S. atrovirens*, and frequently even by females of that species. Mating behavior seemed to be of the assault type described by Spieth (1974). Copulation lasted anywhere from a few minutes to well over an hour. During mating the pair remained relatively inactive, although females frequently fed intermittently. During copulation the male assumed a position dorsal to the female and facing in the same direction. The preoviposition period in 4 laboratory-reared females ranged between 4 and 7 days and averaged 6 days.

An indication of the potential fecundity of *S. atrovirens* was obtained by determining the number of developing eggs per ovariole and the total number of ovarioles in each of 8 females that were collected in northeastern Ohio during August, 1979. The number of ovarioles per female varied between 28 and 36 and averaged 31.3. The number of detectable oocytes per ovariole averaged 7.8 and ranged between 6 and 11. Assuming that each ovariole is capable of producing 8 eggs during the life of a female and that each female possesses 31 ovarioles, the average fecundity is around 250 eggs. The range would be between 168 ( $28 \times 6$ ) and 396 ( $36 \times 11$ ). Actual egg counts obtained from field-collected and laboratory-reared females were considerably less than the values given above. Two females collected in nature deposited an average of only 40 eggs each in the breeding chambers.

In the laboratory rearings, females oviposited into monocultures of *Anabaena variabilis*, *A. sp.*, *Cylindrospermum* sp., *Oscillatoria* spp., and *Navicula pelliculosa*. In contrast, no eggs were deposited in cultures of *Chlorella vulgaris*. Eggs were widely scattered over the algal substrate and no clumping was noted. They were generally oriented horizontally and occasionally were completely imbedded in the alga mat. The eggs were elongate-ovoid in shape, lacked terminal filaments, and possessed a distinct pinkish cast. The incubation period varied between 1 and 2 days and averaged 1.8 days ( $n = 45$ ) in the laboratory rearings.

Eggs in nature were usually found in floating mats dominated by blue-green algae. In Ohio, they were found in a small mat of *Oscillatoria* sp. growing in a shallow, mud-bottomed rain pool having a surface area of less than 2 m<sup>2</sup>. They were also taken abundantly in a mixed mat of *Anabaena* and *Spirogyra* that was floating on the surface of a small marsh. In Montana, eggs were discovered in a floating mat composed largely of species of *Nostoc* and *Cylindrospermum* located in shallow water along the south shore of Flathead Lake. A few filamentous green algae were present in the mat

also, and unicellular interstitial algae, particularly diatoms, were abundant. Also included in the mats were floating fragments of macrophytes, particularly debris derived from *Typha* and *Potamogeton*. A series of 3 petri dish samples of the mat was taken along a transect extending from the sand shore to the far edge of the algal growth. Very few *Setacera* eggs were found within algae occurring on the moist shoreline sand, whereas they were equally abundant in samples taken at the water's edge and 2 m away from the shore. Eggs were particularly common in growths of *Nostoc* but relatively uncommon in colonies of *Cylindrospermum*.

Newly hatched larvae quickly began ingesting algae and seemingly preferred small unicells such as those of various species of diatoms. Older larvae apparently could utilize a broader range of algal species and frequently ingested trichomes of blue-green algae. A gut sample of a nearly mature larva collected in an *Oscillatoria* mat in Ohio contained numerous trichomes of that genus but also included considerable quantities of detritus. The gut of a third-instar larva taken from the *Nostoc-Cylindrospermum* mat at Flathead Lake, Mont. contained many trichomes of *Nostoc*, several fragments of *Cylindrospermum*, numerous cells of *Cosmarium*, and a few specimens of *Oocystis*, *Scenedesmus*, *Navicula*, and *Pediastrum*. Whether all these algal taxa were being digested and assimilated was not determined. To determine whether larvae preferred *Cylindrospermum* or *Nostoc*, 5 second instars were placed in the center of a petri dish which contained 2 samples of each of those 2 genera. The observations began at 3 PM and ended 6 hours later. By the end of the first hour 4 larvae were on *Nostoc* and only one was on *Cylindrospermum*, a situation that did not change during the subsequent 5 hours. A second test involved *Anabaena* sp., the larval food of *S. pacifica* at a highly alkaline (pH 9.4) pond located south of Ronan, Mont. Ten second- and third-instar larvae of *S. atrovirens* were placed in a dish containing *Anabaena*, and 10 others were placed in *Nostoc* collected at the Flathead Lake site. Larvae seemingly fed equally well in both algal genera, suggesting that larvae of these 2 *Setacera* species are not trophically segregated.

Examination of floating balls of *Nostoc* collected along the south shores of Flathead Lake revealed that the algal colonies were noticeably damaged due to larvae burrowing through the gelatinous matrix. The colonies became riddled with holes and soon assumed a shredded, frayed appearance. Shortly thereafter, they lost any semblance of cohesiveness and disappeared.

Larvae frequently fed while completely submerged but seemingly had to return to the water surface periodically to place the posterior spiracles in contact with air. This generally presented no problem, as algal mats in nature typically floated at or near the surface. Similar behavior was noted in *S. micans* in Europe by Beyer (1939).

Table 1 summarizes data obtained in laboratory feeding tests utilizing



Table 1. Results of larval feeding tests for *S. atrovirens* using different algal monocultures.

Alga	n	Percent Reaching Different Life Stages			
		2L	3L	P	A
Cyanophyceae					
<i>Anabaena variabilis</i>	30	100	100	97	97
<i>Anabaena</i> sp.	10	100	80	80	80
<i>Cylindrospermum</i> sp.	30	100	70	50	40
<i>Gloeocapsa</i> sp.	30	97	83	40	0
<i>Lyngbya</i> sp.	30	97	90	46	27
<i>Nostoc commune</i>	30	100	33	20	20
<i>Oscillatoria chalybea</i>	30	43	7	0	0
<i>Oscillatoria tenuis</i>	30	100	100	97	47
<i>Phormidium</i> sp.	30	100	97	40	7
<i>Synechococcus leopoliensis</i>	30	100	93	10	0
Chlorophyceae					
<i>Chlamydomonas</i> sp.	20	100	85	35	20
<i>Chlorella vulgaris</i>	30	0	0	0	0
Bacillariophyceae					
<i>Navicula pelliculosa</i>	30	100	100	77	50
Xanthophyceae					
<i>Botrydiopsis alpina</i>	10	100	10	10	0

unialgal cultures. Larvae completed development and eventually produced adults in monocultures of certain blue-green species as well as in cultures of *Chlamydomonas* sp. and *Navicula pelliculosa*. In contrast, no larval development occurred in cultures of *Chlorella vulgaris*. Interestingly, not all species of blue-greens permitted development, as no adults were obtained in cultures of *Synechococcus leopoliensis*, *Gloeocapsa* sp., and *O. chalybea*. The *Oscillatoria* tests were particularly intriguing in that *O. tenuis* seemed quite satisfactory as a larval food, whereas *O. chalybea* gave very poor growth.

Table 2 presents data on the duration of the larval and pupal periods in those monocultures that permitted complete development. Developmental times were shortest in *A. variabilis* (14 days); somewhat longer in *Anabaena* sp., *Cylindrospermum* sp., *Chlamydomonas* sp., *Lyngbya* sp., *Phormidium* sp., and *N. pelliculosa* (17–21 days), and longest in *Nostoc commune* (24.9 days).

Shortly before forming puparia, larvae moved away from the algal colonies and sought out floating or slightly submerged stems or narrow leaves of such aquatic macrophytes as *Potamogeton* and *Myriophyllum*. Occasionally, larvae attached themselves to filaments of green algae. The last proleg was used to attach the mature larva to the support. Interestingly,

Table 2. Developmental times in days for *S. atrovirens* using different algal monocultures.

Algal	Larval Period		Pupal Period		Combined Period	
	$\bar{x}$	<i>s</i>	$\bar{x}$	<i>s</i>	$\bar{x}$	<i>s</i>
<i>Anabaena variabilis</i> ( <i>n</i> = 29)	6.9	0.37	7.2	0.75	14.1	0.92
<i>Anabaena</i> sp. ( <i>n</i> = 8)	12.8	0.46	7.5	0.93	20.3	1.39
<i>Cylindrospermum</i> sp. ( <i>n</i> = 12)	13.2	1.60	6.7	1.21	19.9	0.90
<i>Nostoc commune</i> ( <i>n</i> = 7)	17.4	0.98	7.5	0.79	24.9	0.90
<i>Lyngbya</i> sp. ( <i>n</i> = 1)	10.0	—	7.0	—	17.0	—
<i>Phormidium</i> sp. ( <i>n</i> = 1)	10.0	—	7.0	—	17.0	—
<i>Chlamydomonas</i> sp. ( <i>n</i> = 1)	14.0	—	7.0	—	21.0	—
<i>Navicula pelliculosa</i> ( <i>n</i> = 10)	9.6	0.84	7.4	0.84	17.0	1.15

many puparia were formed below the water surface and thus out of contact with atmospheric air. Submergence had no apparent effect on pupal development, as numerous adults were obtained from puparia that were as much as 10 cm below the surface. Under laboratory conditions, the pupal period lasted about 7 days (Table 3).

Several successful attacks on *Setacera* larvae by larvae of water scavenger beetles (Hydrophilidae) were noted in field-collected samples of algal mats. Hydrophilid larvae were quite abundant in nearly all of the mats examined and probably served as the primary predator of the larval stages of the fly, although nymphs of damselflies may also have affected larval populations. Several adults of a species of chalcidoid wasp were reared from a few puparia that had been collected in nature.

With a preoviposition period of 6 days, an incubation period of 2 days, a larval period of 10 days, and a pupal period of 7 days, the life cycle can be completed in approximately 25 days. This suggests that at least 4 generations are produced in the northern states during a warm season lasting from late May to late September. Overwintering probably occurs as adults in a state of reproductive diapause (Beyer, 1939). Examination of 8 females collected in nature on October 10, 1980, revealed undeveloped ovaries and numerous fat deposits within the abdominal cavity. The latest record for a female in northern Ohio was obtained on November 7, but no effort to discover overwintering adults in nature has been made. The first seasonal record for an adult was obtained on April 5.

#### OBSERVATIONS ON OTHER SPECIES OF *SETACERA*

##### *Setacera durani* (Cresson)

Adults of this species were swept from the surface of an algal mat that had developed in Sonoita Creek at Patagonia, Ariz. The stream was receiving effluent from a sewage lagoon with the result that blue-green algae and

Table 3. Life cycle data for *S. atrovirens* in northeastern Ohio. Rearings maintained at 22°C, with *Anabaena variabilis* serving as adult and larval food.

Flight Period	Early April–early November (?)
Premating Period	2–4 days
Preoviposition Period	4–7 days
Incubation Period	2 days
Larval Period	5–7 days
Pupal Period	7–8 days
Length of Life Cycle	18–24 days
Fecundity	168–396 eggs/female
Number of generations/year	4+

other algal taxa had developed extensive growths in and along the water-course. Several larvae and puparia were collected from the mat.

### *Setacera pacifica* (Cresson)

Large populations of this western species were found during the summer of 1973 and 1980 at highly alkaline ponds located at the Ninepipes Wildlife Refuge near Ronan, Mont. The pH of the study pond averaged above 9 during both summers, and the water contained large quantities of carbonate and bicarbonate ions. Algae were abundant, particularly species of the blue-green genera *Anabaena* and *Oscillatoria*, and formed extensive floating mats in the shallow nearshore water. Other algal genera found in the mats were *Navicula*, *Pandorina*, *Euglena*, *Cosmarium*, *Staurastrum*, *Scenedesmus*, and *Tetraedron*. The shores became increasingly exposed as the pond dried during the months of July and August, with the result that a wide band of highly alkaline mud developed around the open water. Aquatic plants were abundant, particularly hornwort (*Ceratophyllum demersum* L.), water-milfoil (*Myriophyllum spicatum* L.), and pondweed (*Potamogeton pectinatus* L., *P. zosteriformis* Fernald).

Other species of Ephydridae repeatedly collected at the alkaline ponds were *Paracoenia bisetosa* (Coquillett), *Lamproscatella muria* Mathis, *Scatella paludum* (Meigen), *Scatophila despecta* (Haliday), *Discocerina obscurella* (Fallén), and *Hydrellia* spp. Occasionally, *Psilopa olga* Cresson and *Philotelma alaskense* Cresson also appeared. The commonest species was *P. bisetosa*, which occurred by the thousands on the muddy shorelines. Except for a species of *Hydrellia*, whose larvae mined the leaves of pondweed, all of the associated species were far more abundant on shoreline muds than on the floating algal mats. To determine the microspatial distribution of adults of *P. bisetosa* and *S. pacifica*, 5 pan traps containing water and a detergent (Grigarick, 1959) were placed along a transect perpendicular to the shoreline. One pan was placed on the mud shore, one was at the



shoreline, and 3 were on the floating algal mat 0.5, 1.0, and 2.0 m away from the shoreline, respectively. They were positioned at the pond after sunset and were collected 24 hours later. The results are given below:

Pan I (on shore mud): 29 *Setacera*, 67 *Paracoenia*

Pan II (at shoreline): 169 *Setacera*, 134 *Paracoenia*

Pan III (0.5 m from shoreline): 111 *Setacera*, 24 *Paracoenia*

Pan IV (1.0 m from shoreline): 48 *Setacera*, 12 *Paracoenia*

Pan V (2.0 m from shoreline): 102 *Setacera*, 45 *Paracoenia*

Although the 2 species showed considerable spatial overlap, *S. pacifica* was most abundant on the floating mat while *P. bisetosa* reached its greatest abundance on the organic-rich mud of the shoreline. Interestingly, very few larvae of *Paracoenia* were found in the offshore algal mats. Conversely, no *Setacera* larvae were present in samples of the shore mud, even though they were fairly common in pieces of the algal mat that had been stranded on the mud by dropping water levels.

Eggs and larvae of *S. pacifica* were abundant in the algal mats, particularly in areas where *Anabaena* formed conspicuous gelatinous growths. The eggs possessed a pinkish color and frequently were imbedded in the mat. As in *S. atrovirens*, no clumping of eggs was noted. The incubation period of 8 eggs lasted an average of 2.3 days in a laboratory rearing.

Larvae at the alkaline pool were not restricted to *Anabaena* colonies, as numerous individuals were found within a mat composed largely of a species of the filamentous green alga *Rhizoclonium*. Also present in this mat were abundant cells of the diatom genera *Navicula* and *Synedra* and the desmid genera *Closterium*, *Cosmarium*, and *Staurastrum*. Examination of the gut contents of 2 third-instar larvae revealed a nearly pure assemblage of *Cosmarium* cells. Only a few cells of the other genera of desmids were present, and there were no fragments of the alga genus *Rhizoclonium*. The gut of another third-instar larva collected elsewhere in the mat contained numerous cells of *Cosmarium*, plus representatives of *Cymbella* (diatom), *Scenedesmus* (green alga) and the blue-green genera *Chroococcus* and *Merismopedia*. Laboratory observations of a larva collected in the *Rhizoclonium* mat showed that it moved along the filaments of that alga while scraping off epiphytic algal cells with its mouthparts.

Larvae collected from mats dominated by *Anabaena* definitely were ingesting trichomes of that alga as determined by examination of the contents of 2 nearly mature larvae. However, other algal genera were also present in the guts, such as *Chroococcus*, *Cosmarium*, and *Staurastrum*. Laboratory-reared larvae also freely ingested trichomes of a species of *Nostoc* that was serving as the primary food of *S. atrovirens* along the shores of Flathead Lake.

As those of *S. atrovirens*, larvae occasionally fed below the water surface

but returned periodically to the surface to renew their air supply. However, most larvae retained contact with atmospheric air via their posterior spiracles while feeding within the algal mats. The larval period of 6 laboratory-reared larvae that had fed on *Anabaena* averaged 10 days.

Puparia in nature were affixed by their last abdominal proleg to thread-like pieces of aquatic macrophytes or to filaments of algae. Two 0.3 m<sup>2</sup> samples of potential substrate for puparia were taken in the pond whose depth at the point of sampling was 0.2 meters. Sample I consisted largely of algal filaments, whereas sample II contained both algal filaments and several leaves and stems of *Ceratophyllum*, *Myriophyllum*, and *Potamogeton*. Sample I contained 11 larvae and 3 puparia, whereas sample II produced 39 larvae and 28 puparia. These results plus general field observations suggest that mature larvae rarely attach themselves to algal strands but rather become affixed to narrow-leaved macrophytes. In sample II, all 28 puparia were attached to either *Ceratophyllum* or *Myriophyllum*, even though *Potamogeton* was equally abundant. Similar results were obtained elsewhere in the study site.

Puparia frequently were formed below the water surface and thus out of contact with atmospheric air. The greatest depth for attachment was approximately 10 cm below the surface of water that was 30 cm deep. Adults successfully escaped from these puparia. In the laboratory rearings, the pupal period lasted 6–7 days for males and 7–8 days for females ( $n = 10$ ).

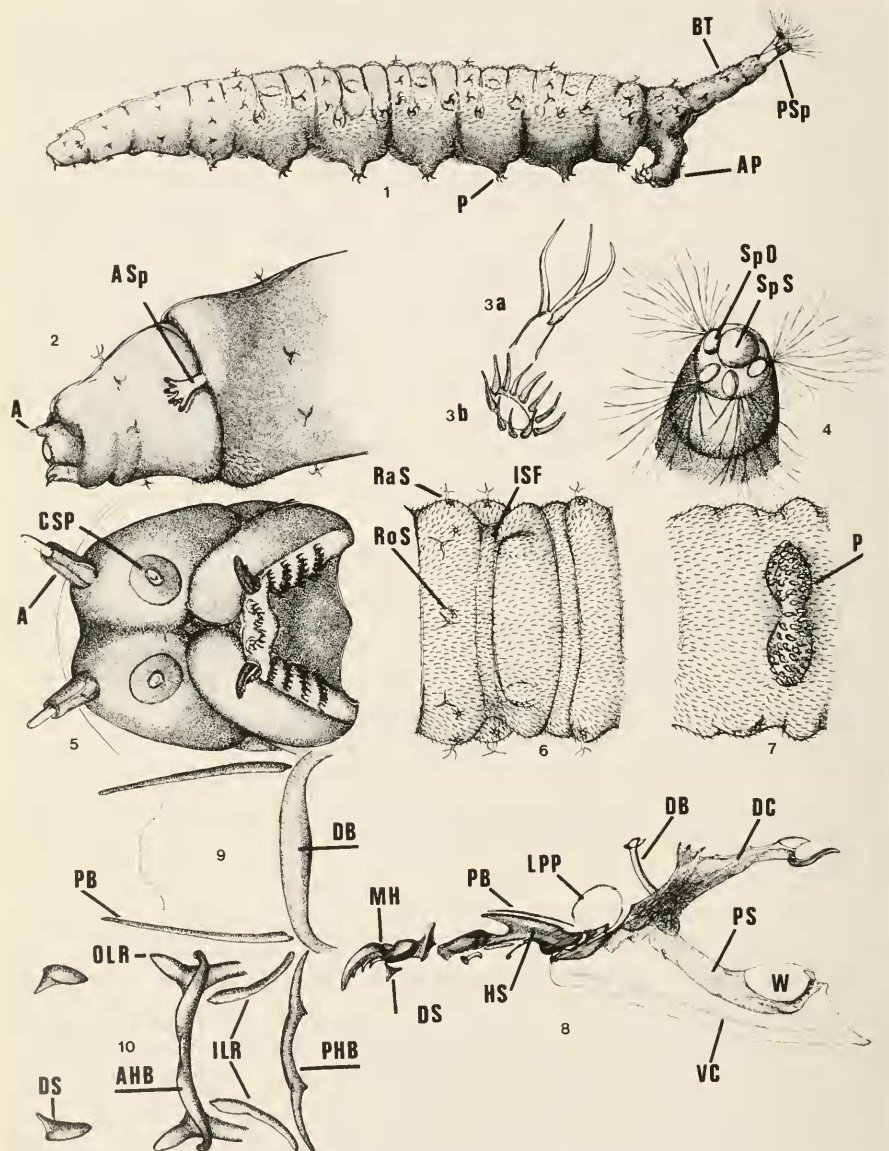
Enemies of *S. pacifica* included parasitic nematodes that were in the abdominal cavities of adults, hydrophilid larvae that preyed on the larval stages, and small chalcidoid wasps that emerged from the puparia.

As in *S. atrovirens*, there were several generations a year, with considerable overlapping of generations. The total life cycle could be completed in 25–30 days.

#### DESCRIPTIONS OF IMMATURE STAGES OF *SETACERA ATROVIRENS*

Egg (Fig. 13).—Length: 0.68–0.75 mm,  $\bar{x} = 0.70$ , width: 0.23–0.26 mm,  $\bar{x} = 0.25$  ( $n = 10$ ). Elongate, ellipsoidal to cylindrical, both ends rounded; chorion appearing minutely papillose micropyle terminal on small papilla, micropylar end bluntly rounded, opposite end somewhat more tapering; living embryo with faint pinkish color.

Mature third-instar Larva (Fig. 1).—Length: 10.5–14.0 mm,  $\bar{x} = 12.0$ ; width: 1.7–2.0 mm,  $\bar{x} = 1.8$  ( $n = 5$ ). Elongate, nearly cylindrical, both ends tapering, posterior end telescoping and forming apically branched breathing tube. Integument nearly concolorous and transparent, without distinct pattern; surface densely covered by somewhat darkened, elongate spinules, no spinules broadened (Fig. 6); integument of each segment bearing 2 kinds of sensilla, each rayed sensillum with elongate base and 3–4 apical branches



Figs. 1-10. *Setacera atrovirens*, mature larva. 1, Lateral habitus. 2, Lateral view of anterior end. 3a, Rayed sensillum. 3b, Rosette sensillum. 4, Posterior spiracle. 5, Facial mask. 6, Dorsum of segment 8. 7, Venter of segment 8. 8, Lateral view of cephalopharyngeal skeleton. 9, Dorsal view of parastomal bars and dorsal bridge. 10, Ventral view of hypostomal and associated sclerites. Abbreviations: A = antenna; AHB = anterior hypostomal bridge; AP = anal proleg; ASp = anterior spiracle; BT = breathing tube; CSP = circular sensory plate; DB = dorsal bridge; DC = dorsal cornu; DS = dentate sclerite; HS = hypostomal sclerite; ILR = in-

(Fig. 3a), each rosette sensillum very short and bearing several narrow branches apically (Fig. 3b). Prolegs present on venter of segments 5–12, anal proleg largest, all prolegs bearing heavy, recurved crochets apically (Fig. 7). Segment 1 (pseudocephalic) (Fig. 2, 5) frequently invaginated, bearing antennae apicodorsally, circular sensory plate apicoventrally, and facial mask ventrally; antennae elongate, appearing 2-segmented; circular sensory plates with rims unbroken, each plate bearing few peg-like structures; facial mask (Fig. 5) with several rows of comb-like structures. Segment 2 (prothoracic) spinulose, bearing anterior spiracles posterolaterally; each spiracle (Fig. 2) somewhat elongate and bearing 3–4 finger-like papillae apically. Segments 3 and 4 very similar, densely spinulose, and bearing prolegs ventrally; each segment with 4 rayed sensilla (Fig. 1), one rosette sensillum next to each dorsal, dorsolateral, and ventrolateral rayed sensillum. Segment 12 (caudal) bearing breathing tube posteriorly and anal proleg and perianal pad ventrally (Fig. 15); breathing tube branched apically, with branches capped by spiracular plates, each spiracular plate (Fig. 4) bearing 4 semi-oval spiracular openings, circular scar, and 4 highly branched spiracular processes; perianal pad at apex of anal proleg posterior to crochets, pad nearly circular (Fig. 16); anal proleg large and somewhat curved forward (Fig. 15).

Cephalopharyngeal skeleton (Fig. 8).—Length: 0.60–0.65 mm,  $\bar{x}$  = 0.62 ( $n$  = 5). Mouthhooks paired, not connected dorsally; hook part slender in lateral view, broader in dorsal view and bordered by several accessory teeth; basal part narrow, with indication of elongate window. Dentate sclerite below basal part of each mouthhook narrowly triangular. Ligulate sclerite narrow and elongate. Hypostomal sclerite (Fig. 10) composed of 2 lateral rods seemingly connected by 2 narrow and strap-like hypostomal bridges, anterior bridge somewhat broader than posterior bridge. Epistomal sclerite broad, poorly pigmented, and fenestrate anteriorly. Parastomal bars (Fig. 9), arising near but not connected to anterior border of pharyngeal sclerite, running forward between and dorsal to hypostomal sclerite, bars not connected to each other or to epistomal sclerite anteriorly. Inner longitudinal rods of hypostomal sclerite converging anteriorly (Fig. 10). Pharyngeal sclerite (Fig. 8) rather deeply pigmented; dorsal cornua slender, connected anteriorly by dorsal bridge; bridge narrow, with few small windows (Fig. 9);

---

ner longitudinal rod; ISF = intrasegmental fold; LPP = lateral pharyngeal process; MH = mouthhook; OLR = outer longitudinal rod; P = proleg; PB = parastomal bar; PS = pharyngeal sclerite; PHB = posterior hypostomal bridge; PSp = posterior spiracle; RaS = rayed sensillum; RoS = rosette sensillum; SpO = spiracular opening; SpS = spiracular scar; VC = ventral cornu; W = window.



ventral cornua broader, each with large window posteroapically; subcircular lateral process arising from anterior margin of pharyngeal sclerite above parastomal bars; floor of pharyngeal sclerite with 9 ridges (Fig. 14), lateral 2 ridges incomplete, remaining 7 ridges each with well-developed lateral lamellae apically that form filtering surface.

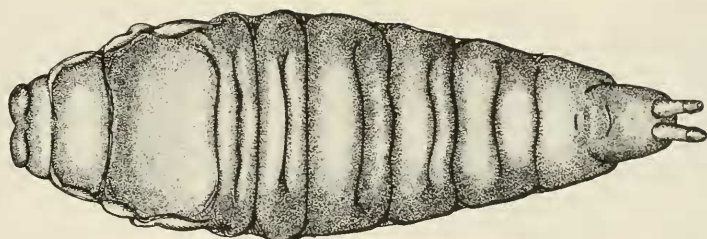
Puparium (Fig. 11, 12).—Length: 7.5–8.0 mm, ( $\bar{x}$  = 7.8; width: 1.4–1.8 mm,  $\bar{x}$  = 1.6 ( $n$  = 5). Somewhat swollen at midlength, with both ends tapering and upturned; anterior end invaginated, bearing anterior spiracles laterally; posterior end elongated into breathing tube. Prolegs on segments 5–11 somewhat reduced compared to larva but bearing distinct crochets apically; anal proleg largest, curved forward and frequently attaching puparium to narrow-leaved macrophyte or algal filament. Integument nearly concolorous brown, without dorsal pattern, densely spinulose, no spinules broadened. Perianal pad somewhat invaginated, subcircular.

### DISCUSSION

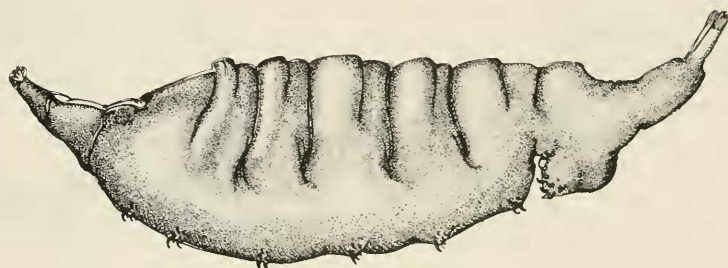
Species of *Setacera* apparently are ecologically unified by their preference for the floating algal-mat habitat. However, little information is available concerning ecological isolation among the eight species occurring in North America. There are indications that some species prefer lentic habitats that have particular water chemistries. For example, *S. atrovirens* has been found most frequently in freshwater habitats with low alkalinity, whereas *S. pacifica* apparently prefers waters of high alkalinity. Thus, these two species may be segregated by habitat. Certainly they do not seem to be segregated trophically, as the larvae of both species readily fed upon and completed development on a wide variety of algal foods. Furthermore, in laboratory tests, larvae of *S. atrovirens* consumed *Anabaena*, the blue-green algal genus heavily grazed in nature by *S. pacifica*. Similarly, *S. pacifica* developed readily on cultures of *Nostoc*, the preferred larval food of *S. atrovirens* at Flathead Lake. Equally obvious is that these two species are not separated temporally, as both occur throughout the warm season and are multivoltine.

Results of the larval food tests involving *S. atrovirens* and 14 species of algae belonging to four classes (Table 1) suggest that larvae of this species are rather generalized trophically. Nine species of 8 genera of 3 algal classes permitted complete larval growth. These data suggested that *S. atrovirens* may be slightly less generalized than *Scatella stagnalis* (Fallén), as that species was able to attain the adult stage on 13 algal species (Zack and Foote, 1978). Moreover, the latter species was able to utilize certain algal taxa that are seemingly unsuitable as larval foods for *S. atrovirens* (e.g., *Gloeocapsa*, *Chlorella*, *Botrydiopsis*). However, larvae of *S. stagnalis* developed very poorly on cultures of *Cylindrospermum* and *Nostoc*, genera of blue-green algae which gave excellent growth in *S. atrovirens*.

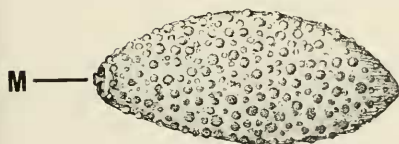




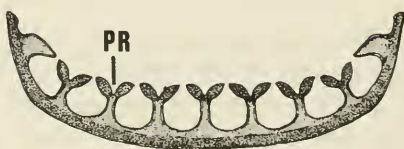
11



12



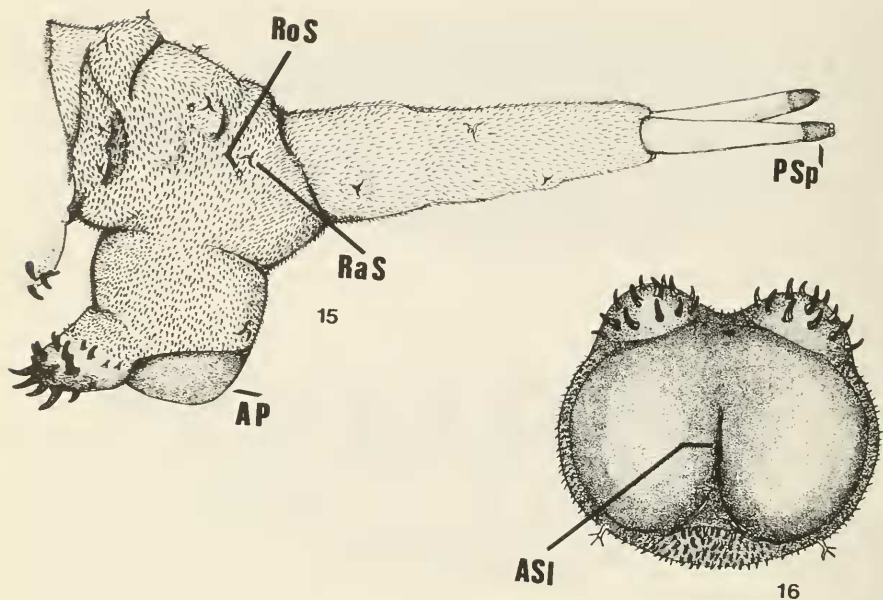
13



14

Figs. 11-14. *Setacera atrovirens*, immature stages. 11, Dorsal view of puparium. 12, Lateral view of puparium. 13, Egg. 14, Cross section of pharyngeal ridges. Abbreviations: M = micropylar end; PR = pharyngeal ridge.

An interesting question concerns the ecological relationship of species of *Setacera* to those of the two other genera of Nearctic Ephydrini associated with floating algal mats. Species of *Cirrula* do not present much of a problem as they are restricted to coastal salt marshes, habitats rarely (if ever) utilized by North American species of *Setacera*. However, there are numerous examples of geographic and perhaps habitat overlap among species of *Ephydra* and *Setacera*. Thus, *S. atrovirens* is sympatric with *E. riparia* Fallén in the



Figs. 15–16. *Setacera atrovirens*, mature larva. 15, Lateral view of caudal segment. 16, Perianal pad. Abbreviations: ASI = anal slit; other abbreviations as in Figs. 1–10.

northeastern states. There may be some habitat segregation in these two species as *E. riparia* is most abundant in saline waters having relatively high chloride ion concentrations, whereas *S. atrovirens* seemingly prefers freshwater habitats having low concentrations of salts. Other examples of geographic co-existence of species in these two genera occur in the western states. Thus, *S. durani* and *E. packardi* Wirth co-exist in southern Arizona, and *S. needhami* occurs with *E. hians* and *E. packardi* in Washington (Zack, personal communication). Once again, however, it is possible that each of these sympatric species is segregated into shallow-water habitats having different water quality. It is significant that neither W. N. Mathis (personal communication), nor R. S. Zack (personal communication), nor I have collected species of both genera regularly in the same habitat.

*Setacera* larvae undoubtedly play several ecological roles in lentic ecosystems. The mechanical damage caused by the burrowing larvae probably accelerates the disruption and eventual decomposition of floating algal mats. Thus, the feeding activities of the larvae must be important in nutrient cycling. The larvae, particularly when abundant, are certainly involved in food chains, as they are utilized by predacious and parasitoid insects and may be consumed by fishes and birds. More practically, the utilization of such heterocystous blue-green algae as *Anabaena*, *Cylindrospermum*, and *Nos-*

*toc* by *Setacera* larvae and adults probably have unsuspected effects on the nitrogen economy of shallow water habitats, as these algae are important nitrogen-fixers (Peters, 1978). Finally, it should be mentioned that the bacterium responsible for Legionnaires disease has been found in floating mats of blue-green algae, where it apparently utilizes algal extracellular products as carbon and energy sources (Tison et al., 1980). This suggests that adults of *Setacera* and other genera of alga mat-visiting Ephydriidae could serve as dispersal agents for this pathogenic bacterium.

#### ACKNOWLEDGMENTS

Appreciation is expressed to W. N. Mathis, Department of Entomology, Smithsonian Institution, for his taxonomic aid and advice. All figures were executed by Tana L. Smith.

#### LITERATURE CITED

- Aldrich, J. M. 1912. The biology of some western species of the dipterous genus *Ephydra*. J. N.Y. Entomol. Soc. 20: 77-90.
- Beyer, A. 1939. Morphologische, ökologische und physiologische Studien an den Larven der Fliegen: *Ephydra riparia* Fallén, *E. micans* Haliday und *Cänia fumosa* Stenhammar. Kiel. Meeresforsch. 3: 265-320.
- Brock, M. L., R. G. Wiegert, and T. D. Brock. 1969. Feeding by *Paracoenia* and *Ephydra* (Diptera: Ephydriidae) on the microorganisms of hot springs. Ecology 50: 192-200.
- Cogan, B. H. 1980. 71. Family Ephydriidae, pp. 655-669. In Crosskey, R. W., ed., Catalogue of the Diptera of the Afrotropical Region. Brit. Mus. Nat. Hist., London.
- Collins, N. 1975. Population biology of a brine fly (Diptera: Ephydriidae) in the presence of abundant algal food. Ecology 56: 1139-1148.
- . 1977. Mechanisms determining the relative abundance of brine flies (Diptera: Ephydriidae) in Yellowstone thermal spring effluents. Can. Entomol. 109: 415-422.
- . 1980a. Population ecology of *Ephydra cinerea* Jones (Diptera: Ephydriidae), the only benthic metazoan of the Great Salt Lake (USA). Hydrobiologia 68: 99-112.
- . 1980b. Developmental responses to food limitation as indicators of environmental conditions for *Ephydra cinerea* Jones (Diptera). Ecology 61: 650-661.
- Deonier, D. L. 1965. Ecological observations on Iowa shore flies (Diptera, Ephydriidae). Proc. Iowa Acad. Sci. 71: 496-510.
- . 1972. Observations on mating, oviposition, and food habits of certain shore flies (Diptera: Ephydriidae). Ohio J. Sci. 72: 22-29.
- . 1979. Introduction—A prospectus of research in Ephydriidae, pp. 1-19. In Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydriidae (Diptera). North Am. Benthol. Soc.
- Foot, B. A. 1977. Utilization of blue-green algae by larvae of shore flies. Environ. Entomol. 6: 812-814.
- . 1981a. Biology and immature stages of *Lytogaster excavata*, a grazer of blue-green algae (Diptera: Ephydriidae). Proc. Entomol. Soc. Wash. 83: 304-315.
- . 1981b. Biology and immature stages of *Pelina truncatula*, a consumer of blue-green algae (Diptera: Ephydriidae). Proc. Entomol. Soc. Wash. 83: 607-619.
- Grigarick, A. A. 1959. Bionomics of the rice leaf miner, *Hydrellia griseola* (Fallén) in California (Diptera: Ephydriidae). Hilgardia 29: 1-80.
- Hennig, W. 1943. Übersicht über bisher bekannten Metamorphosestadien der Ephydriden,

- mit Neubeschreibungen nach Material der Deutschen Limnologischen Sunda-Expedition. Arb. Morph. Taxon Entomol. Berlin-Dahlem 10: 105-138.
- Johannsen, O. A. 1935. Aquatic Diptera. Part II. Orthorrhapha-Brachycera and Cyclorrhapha. N.Y. Agric. Exp. Stn. Mem. 177: 1-62.
- Mathis, W. N. 1982. Studies of Ephydrinae (Diptera: Ephydriidae), VII: Revision of the genus *Setacera* Cresson. Smithson. Contrib. Zool. 350, 57 pp.
- Mathis, W. N. and K. W. Simpson. 1981. Studies of Ephydrinae (Diptera: Ephydriidae), V: The genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America. Smithson. Contrib. Zool. 329: 1-51.
- Nemenz, H. 1960a. Beiträge zur Kenntnis der biologie von *Ephydra cinerea* Jones 1906 (Dipt.). Zool. Anz. 165: 218-226.
- . 1960b. On the osmotic regulation of the larvae of *Ephydra cinerea*. J. Insect Physiol. 4: 38-44.
- Ping, O. 1921. The biology of *Ephydra subopaca* Loew. Mem. Cornell Univ. Agric. Exp. Stn. 49: 557-616.
- Peters, G. A. 1978. Blue-green algae and algal associations. Bioscience 28: 580-585.
- Rohdendorf, B. 1974. The Historical Development of Diptera. Univ. Alberta Press. xv + 360 pp.
- Scheiring, J. F. and B. A. Foote. 1973. Habitat distribution of the shore flies of northeastern Ohio. Ohio J. Sci. 73: 152-166.
- Simpson, K. W. 1973. Biology and immature stages of certain Ephydriidae (Diptera) occurring in North America. Ph.D. Diss., Cornell Univ.
- . 1976. The mature larvae and puparia of *Ephydra* (*Halephydra*) *cinerea* Jones and *Ephydra* (*Hydropyrus*) *hians* Say (Diptera: Ephydriidae). Proc. Entomol. Soc. Wash. 78: 263-269.
- . 1979. Evolution of life histories in the Ephydrini, pp. 99-109. In Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydriidae (Diptera). North Am. Benthol. Soc.
- Spith, H. T. 1974. Courtship behavior in *Drosophila*. Annu. Rev. Entomol. 19: 385-405.
- Starr, R. C. 1978. The Culture Collection of Algae at the University of Texas at Austin. J. Phycol. 14(Suppl.): 47-100.
- Trägårdh, I. 1903. Zur Anatomie und Entwicklungsgeschichte der Larve von *Ephydra riparia* Fallén. Arkiv. Zool. 1: 1-42.
- Tison, D. L., D. H. Pope, W. B. Cherry, and C. B. Fliermans. 1980. Growth of *Legionella pneumophila* in association with blue-green algae (Cyanobacteria). Appl. Environ. Microbiol. 39: 456-459.
- Wirth, W. W. 1965. Family Ephydriidae, pp. 734-759. In Stone, A., et al., eds., A Catalog of the Diptera of America North of Mexico. U.S. Dep. Agric., Agric. Handb. 276.
- . 1968. Family Ephydriidae, pp. 1-43. In Papavero, N., ed., A Catalogue of the Diptera of the Americas South of the United States. Dep. Zool. Sec. Agric. São Paulo, Brazil.
- . 1971. The brine flies of the genus *Ephydra* in North America (Diptera: Ephydriidae). Ann. Entomol. Soc. Am. 64: 357-377.
- . 1975. A revision of the brine flies of the genus *Ephydra* of the Old World (Diptera: Ephydriidae). Entomol. Scand. 6: 11-44.
- Zack, R. S. and B. A. Foote. 1978. Utilization of algal monocultures by larvae of *Scatella stagnalis*. Environ. Entomol. 7: 509-511.
- Zavattari, E. 1921. Ricerche morfologiche ed etologiche sul dittero alofilo *Ephydra bivittata* Loew. R. Comit. Talassogr. Ital. Venezia Mem. 83, 58 pp.